

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3444, 24 pp., 8 figures June 2, 2004

On the Identities of *Colostethus inguinalis* (Cope, 1868) and *C. panamensis* (Dunn, 1933), with Comments on *C. latinasus* (Cope, 1863) (Anura: Dendrobatidae)

TARAN GRANT¹

ABSTRACT

For the past several decades, it has been thought that *Colostethus inguinalis* (Cope, 1868) (type species of *Prostherapis* Cope, 1868) is distributed in the Chocó region of western Colombia and throughout much of Panama. This study shows that *C. inguinalis* is a Colombian endemic known only from the lowlands of the Chocó and Magdalena Valley—an unusual distribution pattern among dendrobatids but one shared with a several other anuran species typically known from the Chocó region. *Colostethus cacerensis* Rivero, 2000 “1995” is argued to be a junior synonym of *C. inguinalis*. The available name for the tetrodotoxin-possessing species found in Panama is *C. panamensis* (Dunn, 1933), which is redescribed. The first record of *C. panamensis* in Colombia is also reported. *Colostethus inguinalis* and *C. panamensis* differ from each other in ventral coloration of adult males and adult females, flank coloration, head coloration, relative tympanum size, and mean adult female snout-vent length. *Colostethus latinasus* (Cope 1863) (type species of *Colostethus* Cope, 1866) is most similar to *C. panamensis* but differs in a variety of characters, including ventral coloration and toe webbing. The exact provenance of the neotype of *C. latinasus* is unclear, but material that agrees closely with it was collected in Panama in the Serranía de Pirre; specimens previously reported as *C. latinasus* from Cerro Malí in the Serranía del Darién are not conspecific with that taxon and represent an undescribed species to be named elsewhere. It is doubtful that the Colombian holotype of *C. latinasus* (lost for over 80 years) was conspecific with the Panamanian neotype, and specimens that agree with the neotype have yet to be discovered in Colombia. Limited

¹ Division of Vertebrate Zoology, Herpetology, American Museum of Natural History; and Department of Ecology, Evolution, and Environmental Biology, Columbia University, 1200 Amsterdam Ave., New York, NY 10027 (grant@amnh.org).

data on tadpole transport provide additional evidence for the validity of several species of *Colostethus* that occur in western Colombia and Central America: Nurse frogs of *C. panamensis* and *C. pratti* (Boulenger, 1899) appear to be exclusively female, of *C. talamancae* (Cope, 1875) both sexes have been reported, and of *C. flotator* (Dunn, 1931), *C. nubicola* (Dunn, 1924), and *Colostethus* sp. from Cerro Malí they appear to be exclusively male. The phylogenetic significance of these observations awaits further analysis.

RESUMEN

Durante las últimas décadas se ha pensado que *Colostethus inguinalis* (Cope, 1868) (la especie típica de *Prostherapis* Cope, 1868) está distribuido ampliamente en la región chochoana del norte de Colombia y gran parte de Panamá. En el presente estudio se demuestra que *C. inguinalis* es una especie endémica de Colombia que se encuentra en las tierras bajas del norte del Chocó y el Valle del Magdalena. Este patrón de distribución es poco usual entre los dendrobátidos pero ocurre en otras especies de anuros típicamente conocidas en el Chocó. *Colostethus cacerensis* Rivero, 2000 "1995" es un sinónimo menor de *C. inguinalis*. El nombre disponible para la especie distribuida en Panamá y que posee tetrodotoxina es *C. panamensis* (Dunn, 1933), la cual se redescubre en el presente artículo. Se reporta el primer registro de *C. panamensis* en el territorio colombiano. *Colostethus inguinalis* difiere de *C. panamensis* en aspectos de coloración ventral de machos y hembras adultos, coloración del flanco, coloración de la cabeza, tamaño relativo del tímpano, y longitud rostro-cloacal promedia de las hembras adultas. *Colostethus latinasus* (Cope, 1863) (la especie típica de *Colostethus* Cope, 1866) comparte su mayor similitud con *C. panamensis* pero difiere de éste en varios caracteres, inclusive la coloración ventral y palmeadura, entre otros. El origen exacto del neotipo de *C. latinasus* es confuso, pero material que concuerda con el neotipo fue obtenido en Panamá en la Serranía de Pirre; otros especímenes de Cerro Malí en la Serranía del Darién reportados anteriormente como *C. latinasus* no son conespecíficos con ese taxón y representan un especie no descrita que será nombrada en otro estudio. Es dudoso que el holotipo colombiano (perdido durante más de 80 años) fuera conespecífico con el neotipo panameño y no se conocen ejemplares conespecíficos con el neotipo en Colombia. Los datos limitados sobre el transporte de larvas ofrecen evidencia adicional sobre la validez de varias especies de *Colostethus* en el occidente colombiano y Centro América: En *C. panamensis* y *C. pratti* (Boulenger, 1899) las hembras transportan los renacuajos, en *C. talamancae* (Cope, 1875) son ambos sexos, y en *C. flotator* (Dunn, 1931), *C. nubicola* (Dunn, 1924) y *Colostethus* sp. de Cerro Malí son los machos. El significado filogenético de estas observaciones requiere mayor análisis.

INTRODUCTION

As evidence accumulates on the phylogeny of dendrobatid frogs, it is important that species identities be examined closely to ensure that the full extent of diversity is taken into account. Of special concern are the type species of *Colostethus* Cope, 1866 and the three genera currently in its synonymy (*Prostherapis* Cope, 1868, *Hyloxalus* Jiménez de la Espada, 1871 "1870", and *Phyllodromus* Jiménez de la Espada, 1871 "1870"), because a monophyletic taxonomy will almost certainly require that *Colostethus* be re delimited. Coloma (1995) clarified the identity of *C. fuliginosus* (Jiménez de la Espada, 1871 "1870"), the type species of *Hyloxalus*, and *C. pulchellus* (Jiménez de la

Espada, 1871 "1870"), the type species of *Phyllodromus*. The identity of *C. latinasus* (Cope, 1863), the type species of *Colostethus*, is simplified somewhat by Savage's (1968) designation of a neotype, but some problems remain and are addressed below. The primary objective of the present study is to clarify the identity of *C. inguinalis* (Cope, 1868), the type species of *Prostherapis*, and, in the process, to resurrect *C. panamensis* (Dunn, 1933), which has been in the synonymy of *C. inguinalis* for nearly half a century.

The Panamanian species known for the last several decades as *Colostethus inguinalis* is among the best studied of all dendrobatids. Duellman (1967) reported its chromosome number ($n = 12$, $2n = 24$). Wells (1980a,

1980b, 1981) performed extensive behavioral studies and reported courtship, reproductive, and developmental data, vocalizations, interspecific interactions, and well-defined spatial organization maintained through agonistic behavior by both sexes (see also Duellman, 1966). Pough and Taigen (1990) included it in their study of metabolic correlates of foraging and social behavior, as did Toft (1981, 1995) and Simon and Toft (1991) in their studies of diet specialization and Toft (1980) in her study of seasonal abundance. And Daly et al. (1994) reported tetrodotoxin in skin secretions of this species (samples from El Valle de Antón and Cerro Campana), which remains unknown in other dendrobates. (See also Ibáñez D. et al., 1999 for general comments.)

In contrast to the many aspects of the biology of this species that have been studied extensively, its taxonomy has not attracted serious attention since the late 1960s. Recent examinations of types and extensive additional material from Panama and Colombia indicate that *C. inguinalis* is endemic to Colombia and that the Panamanian species should be known as *C. panamensis*.

TAXONOMIC AND NOMENCLATURAL HISTORY

Cope (1868) named the new genus and species *Prostherapis inguinalis* on the basis of a single adult female (fig. 1A) taken along Río Truandó in Colombia. Boulenger (1882) reported three more specimens from Colombia, Ecuador, and British Guiana. Peracca (1904) reported numerous specimens from the Río Santiago valley in southeastern Ecuador. Barbour and Noble (1920) reported on additional Peruvian specimens, which they described as having pink flash colors. However, there is no indication that they examined the holotype, and, although they did not provide catalog numbers or locality data, Noble (1926: 9) reported the species to occur in sympatry with *Dendrobates* [now *Epipedobates*] *braccatus*; the pink flash colors and locality data (assuming Noble was referring to the same specimens seen by Barbour and Noble) suggest that the specimens were not conspecific with the northwestern Colombian species. Accordingly, Parker (1935: 506)

concluded that at least some of Boulenger's and all of Barbour and Noble's specimens must have been *Phyllobates* [now *Epipedobates*] *femoralis* (he did not examine their material). Cochran and Goin (1970: 40) concurred that the specimens Barbour and Noble and (presumably) Noble had seen were actually *Prostherapis* [now *Epipedobates*] *femoralis*—although they did not discuss evidence in support of that claim, and Rivero and Serna (1989 “1988”) disputed Cochran and Goin's identification of most of the specimens they had referred to *Colostethus inguinalis* (as *Phyllobates* sensu Cochran, 1966). The identity of Peracca's (1904) specimens has not been reexamined, but it is highly doubtful that they are conspecific with the northwestern Colombian species; Peracca's specimens were collected together with *Epipedobates parvulus* (reported by Peracca as the new species *Prostherapis festae*; see Coloma, 1995).

Subsequent to Barbour and Noble's specimens, no new specimens of *Colostethus inguinalis* were reported until Breder (1946) discussed a number of Panamanian specimens under the name *Prostherapis inguinalis*. Breder also indicated that Dunn (1940) had mistakenly referred specimens of this species to *Hyloxalus fuliginosus* (see also Savage, 1968, and Remarks under *Colostethus panamensis*, below). Evans (1947) reported a single specimen of *Phyllobates inguinalis* from El Valle; although he did not provide specimen numbers, Evans was most likely referring to adult female AMNH 52738 (AMNH 52739 is a conspecific adult male and was also collected by Evans, but only AMNH 52738 is listed on either the geographic or taxonomic index cards used at that time).

In the meantime, Dunn (1933) described *Hyloxalus panamensis* on the basis of seven specimens (holotype shown in fig. 1B) from El Valle de Antón, Panama. Without comment, Dunn (1940) emended the specific name to *panamensis*. Although this is not a justified emendation (fide Articles 32.5 and 33 of ICZN, 1999), a petition has been submitted (Grant et al., in press) to the International Commission on Zoological Nomenclature to validate the emended spelling, and I treat it as valid pending the Commission's

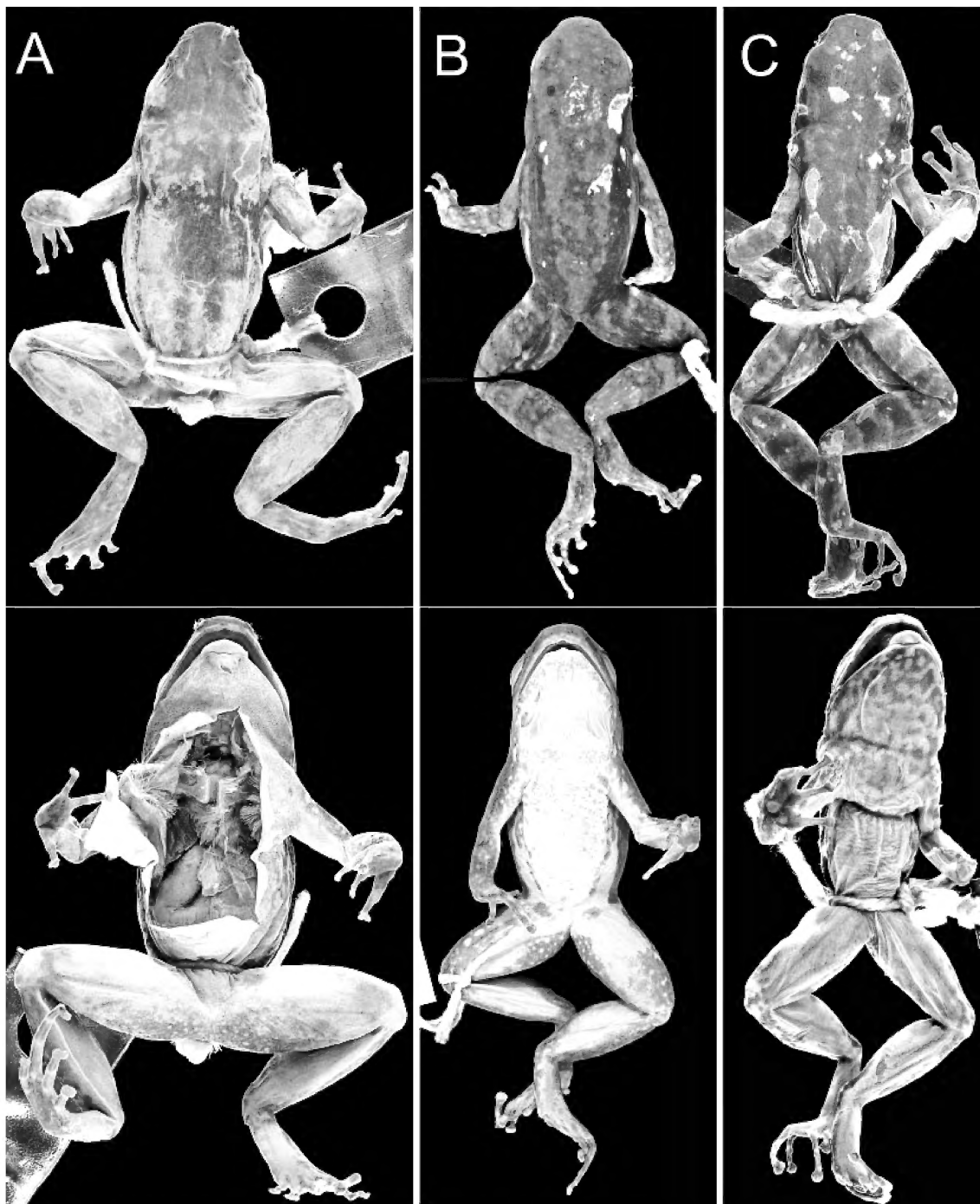


Fig. 1. Dorsal and ventral views of type specimens of three species currently placed in *Colostethus*. **A:** *Prostherapis inguinalis* (holotype, adult female, 27.6 mm SVL, type species of *Prostherapis*), USNM 4349. **B:** *Hyloxalus panamensis* (holotype, adult male, 24.5 mm SVL), MCZ 19209. **C:** *Phyllobates latinasus* (neotype, adult female, 30.3 mm SVL, type species of *Colostethus*), USNM 50198.

decision. Breder (1946) did not treat *Hyloxalus panamensis* except to point out that some of the specimens Dunn (1940) had referred to that taxon were *Phyllobates* [now *Colostethus*] *pratti*.

Until 1957, Dunn followed Noble's (1922, 1923, 1926) scheme of relationships, whereby *Hyloxalus* Jiménez de la Espada, 1871 "1870" was diagnosed as having toe webbing and teeth (Savage, 1968, incorrectly attributed that characterization of *Hyloxalus* to Dunn, 1931), *Phyllobates* Duméril and Bibron, 1841 as having teeth but no toe webbing, and *Dendrobates* Wagler, 1930 as having neither teeth nor toe webbing. Barbour and Noble (1920) had previously concluded that *Prostherapis* was a subjective synonym of *Phyllobates*. After examining the holotype of *Prostherapis inguinalis*, Dunn (1957: 77) concluded that *Hyloxalus* and *Prostherapis* were congeneric and, moreover, that *Prostherapis inguinalis* was "conspecific with the Panamá forms" previously referred to *Hyloxalus*, i.e., *Hyloxalus panamensis*.² Accordingly, *Prostherapis* was removed from the synonymy of *Phyllobates*, *Hyloxalus* became a junior synonym of *Prostherapis*, and *Prostherapis panamensis* passed into the synonymy of *Prostherapis inguinalis*. Nevertheless, Fouquette (1960) reported a new record of *Hyloxalus panamensis*. Heatwole and Sexton (1966) treated the taxon as the subspecies *Phyllobates inguinalis panamensis*. Duellman (1966) recognized *Prostherapis panamensis* as a valid species, but the following year he (Duellman, 1967) recognized *Prostherapis inguinalis*. Savage's (1968) highly influential paper on Central American dendrobatids decisively established that *Prostherapis inguinalis* and *Hyloxalus panamensis* were conspecific. Savage also concluded that *Prostherapis* (including *Hyloxalus*) was a junior synonym of *Colostethus* Cope, 1866, making the Panamanian species *Colostethus inguinalis*. Savage's conclusions were largely adhered to by all subsequent workers, including Edwards (1971) and Silverstone

(1976: 6)—the sole exception being Cochran and Goin (1970), who followed Cochran's (1966) generic arrangement and did not treat *Hyloxalus panamensis*—leading workers to believe *Colostethus inguinalis* to occur from northern Colombia through much of lowland Panama.

MATERIALS AND METHODS

As noted previously (Grant and Rodríguez, 2001), a cladistic delimitation of *Colostethus* is lacking and species are referred to this genus simply because they cannot be assigned to any named clade of dendrobatids. To facilitate species determination, *C. inguinalis* and *C. panamensis* are diagnosed from each other as well as all other currently recognized species of *Colostethus* from Panama and the lowlands of northern Colombia: *C. chocoensis* (Boulenger, 1912), *C. flotator* (Dunn, 1931), *C. imbricolus* Silverstone, 1975, *C. lacrimosus* Myers, 1991, *C. latinasus*, *C. lynchi* Grant, 1998,³ *C. nubicola* (Dunn, 1924), *C. pratti* (Boulenger, 1899), and *C. talamancae* (Cope, 1875).

Measurements were taken to 0.1 mm with dial or digital calipers. Unless otherwise noted, measurements and proportions are given for adults only, as determined by examination of gonads and secondary sex characters. Males with vocal slits on both sides of the mouth were scored as adult, those with only one as subadult, and those lacking slits on both sides as juvenile. Females with expanded, convoluted oviducts and enlarged ova were considered to be adult, those with only weakly expanded, non- or weakly convoluted oviducts and poorly differentiated ova to be subadult, and those with small, undifferenti-

² Although his views were not published until after his death, it appears that Dunn arrived at this conclusion about the identity of the Panamanian species as early as 1947 when he "checked" Evans's (1947) identification of (presumably) AMNH 52738 from El Valle as *Phyllobates inguinalis*.

³ Grant (1998) questioned the veracity of the locality data for the only known specimen of *C. lynchi*, which place it in the Chocoan lowlands of Antioquia. The grounds for questioning the locality were the putative grouping of *C. lynchi* with *C. edwardsi* + *C. ruizi* on the basis of the synapomorphic cloacal sheath (Lynch, 1982) and the fact that the original tag was not on the specimen when it was examined. However, although new material has not been obtained to corroborate the locality data, examination of extensive material of most species of dendrobatids has caused me to doubt the validity of that character, which is also claimed as a synapomorphy of *Nephelobates* (La Marca, 1994). I therefore include *C. lynchi* in the Chocoan fauna for the present purposes.

ated ova and unexpanded, straight oviducts to be juvenile. Statistical summaries of measurements are reported as the mean \pm standard error of the mean, and statistical tests were run using SAS software version 8.02. Toe webbing formulas follow Myers and Duellman (1982; see also Savage and Heyer, 1967, 1997). Ear terminology follows Lynch and Duellman (1997). Diagnostic characters are derived from Edwards (1974), Myers et al. (1991), Coloma (1995), Grant et al. (1997), Grant and Castro-Herrera (1998), and Grant and Rodríguez (2001).

Institutional abbreviations are AMNH (American Museum of Natural History), ANSP (Academy of Natural Sciences of Philadelphia), CSJ (Colegio San José, Medellín), IAvH (Instituto de Investigación de Recursos Biológicos Alexander von Humboldt), ICN (Instituto de Ciencias Naturales, Universidad Nacional de Colombia), KU (University of Kansas Natural History Museum), LACM (Natural History Museum of Los Angeles County), MCZ (Museum of Comparative Zoology, Harvard University), MHUA (Museo de Historia Natural, Universidad de Antioquia), SIUC (Southern Illinois University at Carbondale), UMMZ (University of Michigan Museum of Zoology), USNM (National Museum of Natural History, Smithsonian Institution), and UVC (Universidad del Valle, Cali).

SYSTEMATICS

Colostethus inguinalis (Cope, 1868)

Figures 1A, 2, 3A, 4

Prostherapis inguinalis Cope, 1868: 137. Holotype USNM 4349. Type locality: "river Truando, New Granada [= Colombia]" (p. 138).

Phyllobates inguinalis—Barbour and Noble, 1920: 399 [Based on specimens of *Epipedobates femoralis* fide Parker, 1935]; Cochran, 1966: 65; Cochran and Goin, 1970: 59 (part).

Colostethus inguinalis—Savage, 1968: 751 (part).

Colostethus cacerensis Rivero and Serna, 2000 "1995": 52 (part). Holotype CSJ 1851. Type locality: "Quebrada La Ceiba, Municipio Cáceres, a unos 10 km. de El Jardín atravesando el Río Cauca hacia el Río Nechi, 7 35' N 75 21' O [W], 85 m., Departamento de Antioquia, Colombia"; NEW SYNONYMY.

DIAGNOSIS: A moderate-sized dendrobatid (males to a maximum of about 27 mm SVL,

females to about 30 mm SVL); finger III swollen in adult males; throat and (usually) chest and anterior belly black in adult males, white (unpigmented) or faintly pigmented gray or brown in adult females; black arm band of adult males absent; testes with varying degrees of brown reticulation; toes moderately webbed; pale dorsolateral stripe absent; pale oblique lateral stripe present, extending from groin midway to eye; pale ventrolateral stripe present; median lingual process absent; cloacal tubercles absent.

Colostethus inguinalis is readily distinguished from *C. panamensis* by the solid black throat (black pigmentation extending posteriad onto chest and anterior belly) of adult males, in contrast to the immaculate or faint, irregular stippling or spotting in adult male *C. panamensis* (compare figs. 2 and 6–7). Adult female *C. inguinalis* are distinctly paler ventrally than adult males, being either immaculate or having faint, scattered stippling, whereas adult female *C. panamensis* are distinctly darker ventrally than adult males, being brown with irregular white spots, forming a mottled or reticulated pattern (compare figs. 2 and 6–7). The flank between the ventrolateral and oblique lateral stripes has scattered diffuse white spots and flecks in *C. inguinalis* (most prevalent in females), whereas that region is solid dark brown in *C. panamensis* (fig. 3). The anteroventral half of the tympanum is pale (white or gray) in *C. inguinalis*, whereas the entire tympanum is dark brown in *C. panamensis* (fig. 3). The tympanum of *C. inguinalis* is well defined and larger (32–47% of eye length), whereas that of *C. panamensis* is inconspicuous and smaller (26–41% of eye length). Mean male SVL does not differ significantly between the two species ($t = 1.23$, $P = 0.2221$), but the mean female SVL of 25.94 mm for *C. inguinalis* is significantly less than the 26.84 mm for *C. panamensis* ($t = 2.98$, $P < 0.05$).

Among the other nine named species of *Colostethus* known to occur in Panama and the lowlands of northern Colombia, *C. inguinalis* differs from all but *C. nubicola* and *C. talamancae* in having a solid black throat in adult males. From *C. nubicola* it differs in adult SVL (maximum in *C. nubicola* is about 21 mm for males and 22 mm for females)

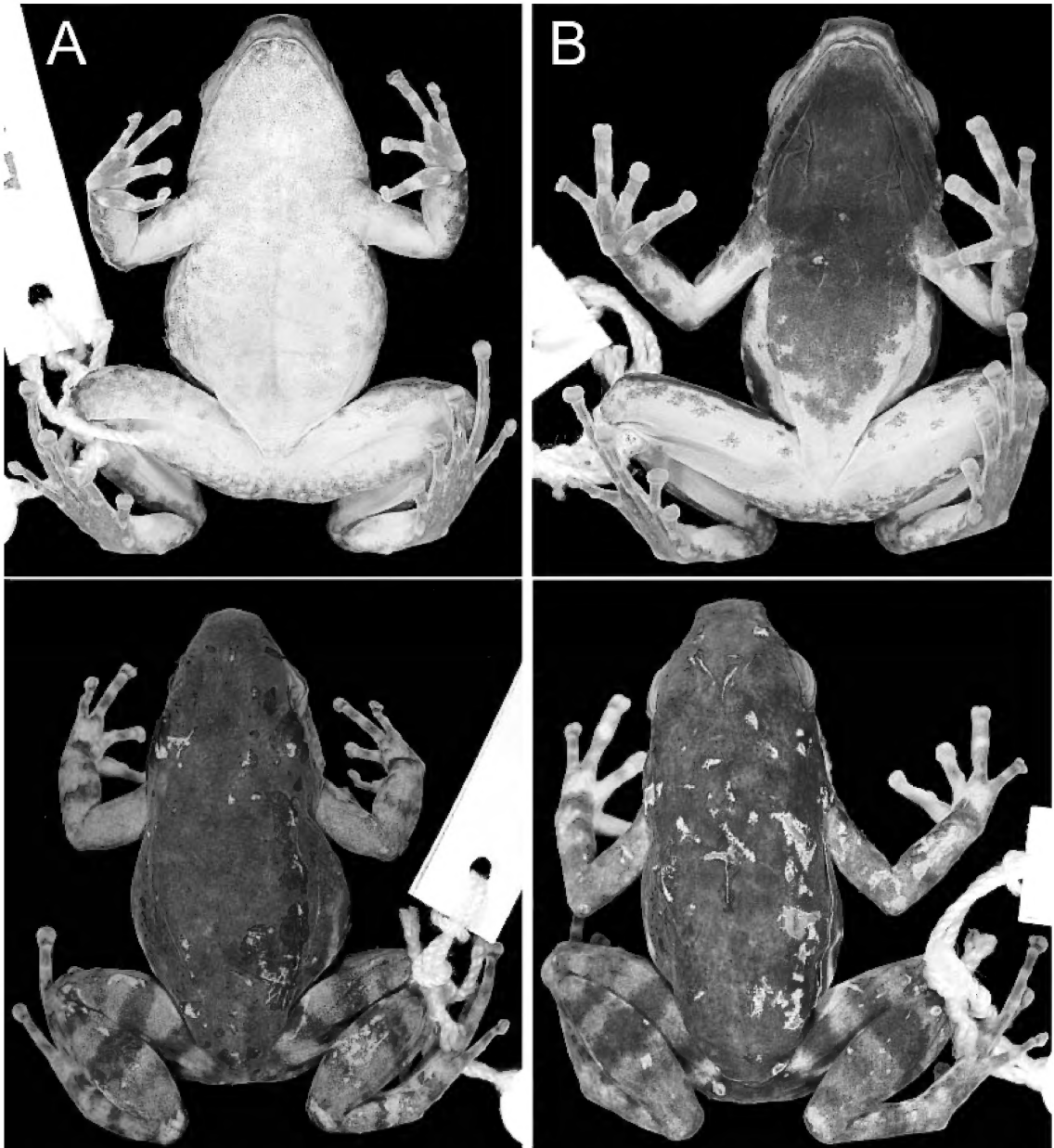


Fig. 2. Ventral and dorsal views of adult female (A: LACM 42409, 28.2 mm SVL, one of the darkest females observed) and adult male (B: LACM 42329, 26.9 mm SVL) specimens of *Colostethus inguinalis*.

and the possession of a partial pale oblique lateral stripe extending from the groin midway to the eye (complete in *C. nubicola*). *Colostethus inguinalis* differs from *C. talamancae* in lacking a pale dorsolateral stripe (present in *C. talamancae*) and possessing a

partial oblique lateral stripe (absent in *C. talamancae*).

Colostethus inguinalis differs from *C. choacoensis* and *C. lacrimosus* in toe webbing (extensive in *C. choacoensis* and *C. lacrimosus*), swelling of the third finger in adult

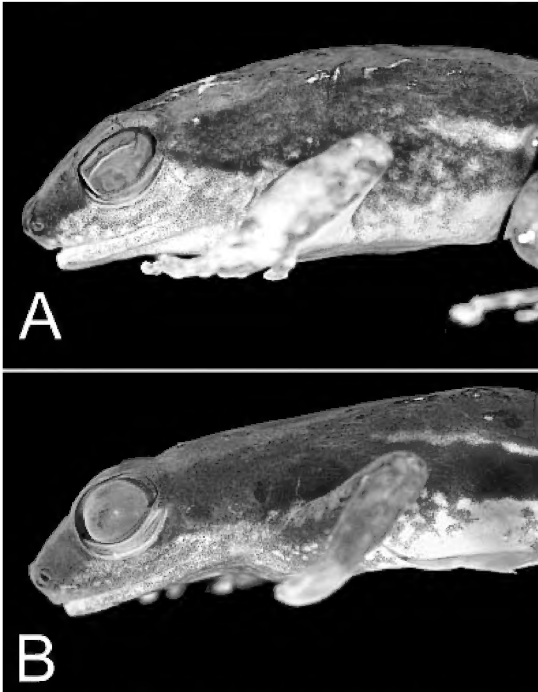


Fig. 3. Lateral views of *Colostethus inguinalis* (A: LACM 42417, adult female, 27.5 mm SVL) and *C. panamensis* (B: AMNH 87297, adult female, 24.9 mm SVL). Note the pale postocular stripe crossing the anteroventral two-thirds of the well-defined tympanum of *C. inguinalis* versus the solid dark brown color of the inconspicuous tympanum of *C. panamensis*.

males (not swollen in *C. chocoensis* and *C. lacrimosus*), adult male throat coloration (immaculate or irregularly and faintly stippled in *C. chocoensis* and *C. lacrimosus*), and possession of a partial pale oblique lateral stripe (absent in *C. chocoensis* and *C. lacrimosus*); it further differs from *C. lacrimosus* in lacking the median lingual process. *Colostethus inguinalis* differs from *C. flotator* in adult male throat coloration (gray in *C. flotator*), adult SVL (maximum in *C. flotator* is about 18 mm for males and 19 mm for females), and in having more extensive toe webbing. It is diagnosed from *C. imbricolus* by ventral coloration (entire venter dark with pale spots in both sexes of *C. imbricolus*), the absence of discrete, bright orange axillary, inguinal, and shank flash marks (present in *C. imbricolus*), and ear color (otic region entirely brown in *C. imbricolus*). *Colostethus inguinalis* differs from *C. latinasus* in degree of toe webbing (absent between all toes or barely detectable between toes III and IV in *C. latinasus*), testis color (white, unpigmented in *C. latinasus*), and ventral coloration (throat and chest brown with white spots forming mottled pattern in *C. latinasus*, darker in adult males; see fig. 8). *Colostethus inguinalis* differs from *C. lynchi* in that the pale oblique lateral stripe extends from the groin only midway to the eye (complete between groin and eye in *C. lynchi*); females of these species differ in ventral coloration (brown with irregular white spots, forming a faint, mottled or reticulated pattern in *C. lynchi*; male *C. lynchi*



Fig. 4. Ontogenetic variation in male ventral coloration of *Colostethus inguinalis*. Left to right: LACM 42522 (subadult, left vocal slit open, 21.0 mm SVL), LACM 42437 (adult, 23.0 mm SVL), LACM 42402 (adult, 23.4 mm SVL), LACM 42334 (adult, 27.4 mm SVL).

unknown). *Colostethus inguinalis* and *C. pratti* differ in adult SVL (maximum known in *C. pratti* is about 24 mm for males and 25 mm for females), toe webbing (absent in *C. pratti*), and adult male throat coloration (pale gray or brown with irregular white spots, forming a faint, mottled or reticulated pattern in *C. pratti*).

MEASUREMENTS OF HOLOTYPE (in mm): The holotype (USNM 4349; fig. 1A) is an adult female with large (ca. 2 mm diameter) pigmented (brown) ova. SVL 27.6; forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow 6.4; hand length from proximal edge of palmar tubercle to tip of third finger 6.6; shank length from outer edges of flexed knee to heel 12.3; foot length from proximal edge of outer metatarsal tubercle to tip of fourth toe 11.5; head width between angle of jaws 9.3; head length diagonally from corner of mouth to tip of snout 8.4; eye length from posterior to anterior corner 3.8; eye to naris distance from anterior corner of eye to center of naris 2.7; distance between centers of nares 3.4; snout length from anterior corner of eye to tip of snout 4.4; interorbital distance 2.6; greatest length of tympanum 1.5.

MORPHOLOGY: Adult males 22.0–27.4 mm SVL ($N = 50$, $\bar{x} = 24.34 \pm 0.22$ mm); testes with brown reticulation, varying from almost immaculate white with brown reticulation medially and anteriorly (e.g., LACM 42332, 42344, 42363) to almost solid brown (e.g., LACM 42434, 42488); extent of melanosis not correlated with SVL, extent of dark ventral coloration, or maturity; testis length approximately one-third eye length. Subadult males LACM 42522 and 42526 21.0 mm and 20.7 mm SVL, respectively. Adult females 22.8–29.7 mm SVL ($N = 54$, $\bar{x} = 25.94 \pm 0.18$ mm). Mature oviducts unpigmented (white), strongly convoluted and swollen; mature ova dark brown, ca. 1.6–2.0 mm diameter. Eighteen subadult females 22.8–26.2 mm SVL, although, given the complete overlap with adult SVLs, it is likely that some or all of these may in fact be reproductively inactive adults.

In preservative, skin of dorsal and lateral surfaces with low, inconspicuous granules, more prominent posteriorly. Ventral surfaces smooth except for extensively wrinkled re-

gion of uninflated vocal sac in adult males. Postrictal (one or two) and preaxillary (one) tubercles moderately enlarged. Head width between angle of jaws 31–36% of SVL, 1.0–1.2 times head length. Interorbital distance 25–33% of head width. Snout sloped, bluntly rounded in dorsal aspect, almost truncate. Canthus rostralis well defined. Loreal region flat or weakly concave, vertical, not sloping to lips. Eye length 34–50% of diagonal head length. Eye–naris distance 54–59% of snout length, 64–76% and 69–79% of eye length in males and females, respectively. Nares slightly protuberant, directed posterodorsad. Tympanum well defined, concealed posterodorsally by low supratympanic bulge formed by overlying superficial slip of m. depressor mandibulae; greatest length of tympanum 34–47% of eye length. Teeth present on maxillary arch.

Hand length 24–29% of SVL and 1.0–1.3 times forearm length. Discs moderately expanded. Finger III clearly swollen along pre- and postaxial surfaces of adult males, most exaggerated along preaxial surface. Preaxial surface of finger II bearing distinct fringe in both sexes but not swollen. Finger III not swollen in adult females or juveniles. Fingers fringed. Metacarpal fold absent. Appressed finger I longer than finger II; fingers II and IV extended to distal edge of distal subarticular tubercle of finger III. Relative lengths of appressed fingers $IV = II < I < III$. Subarticular tubercles 1–1–2–2. Supernumerary tubercles absent. All tubercles strongly protuberant except distal subarticular tubercle of swollen finger III in adult males, in which it is diffuse; subarticular and thenar tubercles elliptical; palmar tubercle subcircular.

Shank and foot length 40–49% and 40–48% of SVL, respectively. Relative lengths of appressed toes $I < II < V < III < IV$. Toe III extended to midlevel of antepenultimate phalanx of toe IV; toe V to middle of penultimate subarticular tubercle. Toe webbing moderate except between IV and V, which is basal or absent; webbing formula $I \frac{1}{2}$ or 2^- $II \frac{1}{2}$ or 2^- $3\frac{1}{2}$ or 3^+ $III \frac{2}{2}$ $3\frac{1}{2}$ or 4 $IV \frac{4}{2}$ 3^- V (when present between IV and V). Fringes strong on all toes. Discs moderately expanded. Tubercles strongly protuberant. Subarticular tubercles 1–1–2–3–2. Inner metatarsal tubercle elongate. Outer metatar-

sal tubercle subcircular, smaller than inner metatarsal tubercle. Medial metatarsal tubercle present in most specimens, ranging from well-defined, conspicuous tubercle (e.g., LACM 42439) to inconspicuous swelling (e.g., LACM 42464); of 100 specimens coded, medial metatarsal tubercle not detected in 7 (see Myers et al., 1991: 23–24). Outer metatarsal fold present in all specimens, not thickened to form low tubercle. Tarsal keel prominent, weakly curved, expanded proximally but not forming tuberclelike protuberance, continuous with inner metatarsal tubercle.

COLOR IN PRESERVATIVE: Dorsum brown with dark brown blotches. Pale dorsolateral stripe absent. Flank brown or (usually) dark brown broken by white or cream oblique lateral stripe extending from groin midway to arm insertion; oblique lateral stripe continuing as series of small white or cream spots to above arm insertion in some specimens (e.g., LACM 42355, right side). Small, diffuse white or cream spots scattered on flank between oblique lateral stripe and wavy white or cream ventrolateral stripe extending between groin and midlevel of arm insertion (i.e., not passing above arm insertion). Dark brown supratympanic bulge demarcated by white or gray extending from eye across anteroventral one-half or three-fifths of tympanum to arm insertion. Face below eye white with extensive evenly stippled melanophores (dark brown in dark specimens, e.g., LACM 42464), often with white (i.e., free of melanophores), curved line immediately below eye. Line of white spots extended along entire upper lip. Loreal region brown or (usually) dark brown.

Ventral coloration sexually dimorphic (fig. 2). Adult males with black throats; black pigmentation extending variably over chest and entire belly, with extent of black pigmentation correlated with SVL (see fig. 4 for ontogeny of male ventral coloration). Females white or cream, immaculate or with faint brown or gray stippling scattered irregularly over throat, chest, and lateral belly. Juveniles immaculate white or cream.

Dorsal surface of upper arm gray or pale brown, lacking transverse bands; anterior and posterior surfaces dark brown, forming dark brown longitudinal stripes, broken ventrally

by tiny white spots; ventrally white or cream. Dorsal, anterior, and posterior surfaces of forearm gray or pale brown with two dark brown transverse bars, one just above wrist, the other midway to elbow, often breaking up posteriorly to form irregular brown blotches; concealed surface of forearm white (free of melanophores; e.g., LACM 42344) or with variable brown and dark brown blotches. Palmar surfaces brown; contact surfaces free of melanophores. Dorsal surface of hand white or cream with dark brown transverse bands on fingers.

Dorsal surface of thigh gray or brown with two or three dark brown transverse bands that align (when limb is flexed) with two or three dark brown transverse bands on gray or brown outer surface of shank and two or three dark brown transverse bands on gray or brown outer surface of foot. Anterior surface of thigh gray or pale brown with well-defined dark brown longitudinal stripe; posterior surface gray or pale brown with dark brown mottling, with mottling often demarcating an irregular pale oblique longitudinal line or elongate spot (e.g., LACM 42331). Ventral surface of thigh and concealed surfaces of shank and foot immaculate white or cream. Plantar surfaces pale brown. Toe webs and fringes with very few scattered melanophores, mostly toward outer edges.

COLOR IN LIFE: Philip A. Silverstone (field notes at LACM) described LACM 42325–42330 in life as follows: Iris gold with black network; small, close-set white dots along the upper lip; broad gold stripe from shoulder under eye to point midway to naris; dark brown longitudinal line along anterior surface of upper arm and along anterior surface of thigh; rest of thigh mottled dull orange and dark brown, with dark brown marks on dorsal surface of thigh; flanks very dark brown, almost black; two orange brown transverse bands on shank; white oblique lateral stripe fading into suffusion of white and gold midway along flank; spots on sides below oblique lateral stripe gold; back dark brown with a few very faint blackish spots; ground color of limbs above dull orange, almost light brown; dark brown line on posterior surface of upper arm; dark brown mottling on posterior surface of forearm; dark brown transverse bands on upper surface of

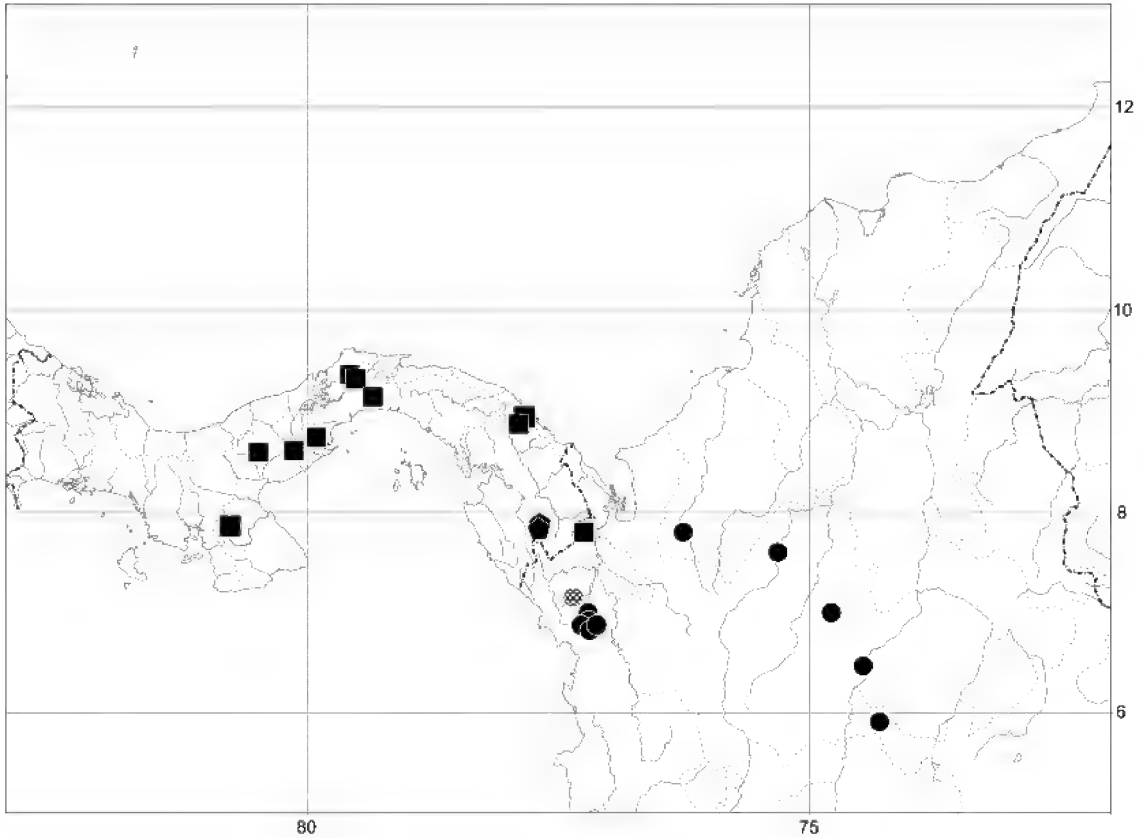


Fig. 5. Map of Panama and northern Colombia showing localities for specimens examined of *Colostethus inguinalis* (circles), *C. latinasus* (pentagons), and *C. panamensis* (squares). The checked circle indicates the approximate locality of the holotype of *C. inguinalis*, which was reported only as “the river Truando, New Granada” (Cope, 1868: 138).

forearm; entirely white ventrally, except a little grayish to pinkish on limbs; some individuals (males) with black on throat, breast, and entire belly except extreme posterior part, leaving white stripe between flank and belly (i.e., ventrolateral stripe).

DISTRIBUTION: *Colostethus inguinalis* occurs in the lowland forests of northwestern and northcentral Colombia up to 400 m elevation (fig. 5). It has been collected in northern Chocó department, immediately north of the western Andean Cordilleras in Antioquia and Córdoba departments, and in the Magdalena Valley of Antioquia and Boyacá departments. Given the absence of any significant geological barriers, and assuming immunity to anthropogenic habitat alteration and destruction, it is likely that *C. inguinalis* ranges continuously throughout this region.

REMARKS: Without discussion, Cochran (1961: 71) listed USNM 4349 as “cotype”; however, Cope’s (1868) description refers only to a single specimen. It seems that Cochran may have mistaken the reference to two specimens under USNM 4349 in the USNM ledger as indicating two type specimens, one of which had been misplaced; the second specimen originally cataloged as USNM 4349 was transferred to USNM 122104 in 1946 and was determined by Jay Savage in 1966 to be *Dendrobates auratus* (Addison Wynn, *in litt.*, 15 May 2003), so there is no question as to which specimen Cope described.

Rivero and Serna (2000 “1995”) named *Colostethus cacerensis* on the basis of 14 specimens from Cáceres in the lowlands of northern Antioquia, immediately north of the

western Andean Cordilleras. They described the species as having a swollen finger III and gray throat in adult males, immaculate venter in adult females, finger I usually longer than finger II, small white spots along upper lip, pale ventrolateral and partial oblique lateral stripes, no dorsolateral stripe, and maximum SVL of 23.2 mm for males and 25.0 mm for females. In all regards⁴ the description of *C. cacerensis* falls well within the variation observed in *C. inguinalis*. I have not examined the holotype of *C. cacerensis*, but I have examined eight paratypes (see appendix 1) collected with the holotype and all are indistinguishable from *C. inguinalis*, with the exception that CSJ 1853 is *C. pratti*. In assigning this species to the synonymy of *C. inguinalis*, I therefore assume that the holotype is conspecific with the majority of the paratypes and not *C. pratti*—an assumption supported by Rivero and Serna's explicit description of the holotype.

Colostethus inguinalis is diurnal and all specimens were collected adjacent to streams. Recordings of the vocalizations of *Colostethus inguinalis* are unavailable, but Philip A. Silverstone described the call of an uncollected male perched on a rock next to a stream near Río Napipí as a "high, loud chip-chip-chip-chip," with 113 calls in 40 seconds, or 2.8 calls per second (7 May 1968, P. A. Silverstone field notes). He described another male by a stream near Río Opogadó as producing 211 calls in 1 minute, followed by 410 calls in 2 minutes, or 3.5 calls per second (13 May 1968, P. A. Silverstone field notes). Although data are too limited for detailed comparisons, this call rate of 2.8–3.5 calls per second differs from the rate of 1.0–1.3 calls per second reported for *C. panamensis* (as *C. inguinalis*) by Wells (1980a).

Colostethus panamensis (Dunn, 1933)

Figures 1B, 3B, 6, 7

Hyloxalus panamensis Dunn, 1933: 69. Holotype: MCZ 19209. Type locality: "El Valle de Anton

in the northwestern corner of the Province of Panama", Panama.

Hyloxalus fuliginosus—Dunn, 1931: 393; Dunn, 1940 (fide Breder, 1946: 405; Savage, 1968: 751).

Hyloxalus panamensis—Dunn, 1940: 109. Emendation (see Grant et al., in press, for petition to validate the emended spelling).

Prostherapis inguinalis—Breder, 1946: 405; Dunn, 1957: 77 (part); Duellman, 1967: 39.

Prostherapis panamensis—Duellman, 1966: 219.

Phyllobates inguinalis—Evans, 1947: 167; Cochran and Goin, 1970: 59 (part).

Prostherapis inguinalis panamensis—Heatwole and Sexton, 1966: 58.

Colostethus inguinalis—Savage, 1968: 751 (part).

Colostethus panamensis—NEW COMBINATION.

DIAGNOSIS: A moderate-sized dendrobatid (males to about 27 mm SVL, females to about 28 mm SVL); finger III swollen in adult males; venter immaculate or with faint, irregular stippling or mottling in adult males; throat conspicuously mottled or reticulated brown or gray in adult females; black arm band of adult males absent; testes white with varying degrees of brown reticulation; toes moderately webbed; pale dorsolateral stripe absent; pale oblique lateral stripe present, extending from groin midway to eye; pale ventrolateral stripe present; median lingual process absent; cloacal tubercles absent.

Colostethus panamensis differs from *C. inguinalis* in being immaculate or having faint, irregular stippling or spotting ventrally in adult males (solid black on throat and extending posteriad onto belly in *C. inguinalis*) and distinctly darker ventral coloration in adult females, either brown with irregular white spots forming a mottled pattern or white with a brown reticulated pattern (immaculate or having faint, scattered stippling in *C. inguinalis*; compare figs. 2 and 6–7). The flank between the ventrolateral and oblique lateral stripes is solid dark brown in *C. panamensis*, whereas that region has scattered diffuse white spots and flecks in *C. inguinalis* (most prevalent in females; fig. 3). The entire tympanum is dark brown in *C. panamensis*, whereas the anteroventral half of the tympanum is pale (white or gray) in *C. inguinalis* (fig. 3). The tympanum of *C. panamensis* is inconspicuous and smaller (26–41% of eye length) than the well-defined and larger (32–47% of eye length) tympanum

⁴ Although I describe the dark ventral coloration of adult males as black and not gray, this difference is merely semantic, as elsewhere Rivero and Serna (1989 "1988", e.g., p. 152) also refer to male *C. inguinalis* as having the throat uniform gray.



Fig. 6. Ventral and dorsal views of *Colostethus panamensis* from El Valle de Antón, Panama. **A:** Adult female (AMNH 124217, 26.5 mm SVL). **B:** Adult male (AMNH 124216, 23.1 mm SVL).



Fig. 7. Ventral and dorsal views of *Colostethus panamensis* from Parque Nacional Natural Los Katios, Colombia. **A:** Adult female (IAvH 3348, 28.2 mm SVL). **B:** Adult male (IAvH 3347, 24.3 mm SVL).

num of *C. inguinalis*. Mean male SVL of the two species does not differ significantly ($t = 1.23$, $P = 0.2221$), but the mean female SVL of 26.84 mm for *C. panamensis* is significantly greater than the 25.94 mm for *C. inguinalis* ($t = 2.98$, $P < 0.05$).

Among the other nine named species of *Colostethus* known to occur in Panama and the lowlands of northern Colombia, *C. panamensis* differs consistently from *C. nubiola* and *C. talamancae* in throat coloration of adult males (solid black in these two spe-

cies) and adult females (immaculate or faintly and irregularly stippled in these two species). It also differs from *C. nubicola* in adult SVL (maximum in *C. nubicola* is about 21 mm for males and 22 mm for females) and having a partial pale oblique lateral stripe extending from the groin midway to the eye (complete in *C. nubicola*). *Colostethus panamensis* also differs from *C. talamancae* in lacking a pale dorsolateral stripe (present in *C. talamancae*) and possessing a partial oblique lateral stripe (absent in *C. talamancae*).

Colostethus panamensis differs from *C. chocoensis* and *C. lacrimosus* in toe webbing (extensive in *C. chocoensis* and *C. lacrimosus*), swelling of finger III in adult males (not swollen in *C. chocoensis* and *C. lacrimosus*), ventral coloration (immaculate or irregularly and faintly stippled and not sexually dimorphic in *C. chocoensis* and *C. lacrimosus*), and possession of a partial pale oblique lateral stripe (absent in *C. chocoensis* and *C. lacrimosus*); it further differs from *C. lacrimosus* in lacking the median lingual process. *Colostethus panamensis* differs from *C. flotator* in adult male throat coloration (gray in *C. flotator*), adult SVL (maximum in *C. flotator* is about 18 mm for males and 19 mm for females), and in having more extensive toe webbing. It is diagnosed from *C. imbricolus* by ventral coloration (entire venter black with pale spots in both sexes of *C. imbricolus*) and the absence of discrete, bright orange axillary, inguinal, and shank flash marks (present in *C. imbricolus*). *Colostethus panamensis* differs from *C. latinasus* in degree of toe webbing (absent between all toes or barely detectable between toes III and IV in *C. latinasus*), testis color (white, unpigmented in *C. latinasus*), and male ventral coloration (throat and chest brown with white spots forming mottled pattern in *C. latinasus*, darker in adult males; see fig. 8). *Colostethus panamensis* differs from *C. lynchi* in that the pale oblique lateral stripe extends from the groin only midway to the eye (extending to eye in *C. lynchi*). *Colostethus panamensis* and *C. pratti* differ in maximum adult SVL (maximum known in *C. pratti* is about 24 mm for males and 25 mm for females), toe webbing (absent in *C. pratti*), and

female ventral coloration (immaculate white in *C. pratti*).

MEASUREMENTS OF HOLOTYPE (IN MM): The holotype (MCZ 19209; fig. 1B) is an undissected adult male with well-developed vocal slits and third fingers strongly swollen along preaxial edges. SVL 24.5; forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow 5.6; hand length from proximal edge of palmar tubercle to tip of third finger 6.4; shank length from outer edges of flexed knee to heel 10.5; foot length from proximal edge of outer metatarsal tubercle to tip of fourth toe 9.9; head width between angle of jaws 7.9; head length diagonally from corner of mouth to tip of snout 7.8; eye length from posterior to anterior corner 3.6; eye to naris distance from anterior corner of eye to center of naris 2.3; distance between centers of nares 3.4; snout length from anterior corner of eye to tip of snout 3.8; interorbital distance 2.6; greatest length of tympanum 1.2.

MORPHOLOGY: Adult males 18.8–27.1 mm SVL ($N = 47$, $\bar{x} = 23.96 \pm 0.22$ mm); testes almost invariably with brown reticulation (of 40 males scored for right testis color, only right testes of IAvH 3347 and 3355 are white, but in both the left testis is brown). Subadult male AMNH 59655 19.5 mm SVL. Adult females 24.9–29.2 mm SVL ($N = 24$, $\bar{x} = 26.84 \pm 0.23$ mm). Mature oviducts unpigmented (white), strongly convoluted and swollen; mature ova dark brown, ca. 1.6 mm diameter. Nineteen subadult females 23.1–27.5 mm SVL, although, given the extensive overlap with adult SVLs, some or all of these may be reproductively inactive adults.

Skin of dorsal and lateral surfaces smooth in preservative, except shanks with very low, inconspicuous granules. Postriatal tubercle elongate, poorly defined or absent in some specimens. Preaxillary tubercle absent, although supratympanic bulge extends close to insertion of arm. Head width between angle of jaws 31–37% of SVL, 1.0–1.2 times head length. Interorbital distance 27–37% of head width. Snout sloped, rounded in dorsal aspect. Canthus rostralis well defined. Loreal region flat or weakly concave, vertical, not sloping to lips. Eye length 39–48% of diagonal head length. Eye–naris distance 53–70% of snout length, 57–74% and 61–78%

of eye length in males and females, respectively. Nares slightly protuberant, directed posterodorsad. Tympanum small, poorly defined; tympanic membrane loosely attached to tympanic annulus; tympanic annulus concealed posterodorsally by overlying m. depressor mandibulae; greatest length of tympanum 26–41% of eye length. Teeth present on maxillary arch.

Hand length 23–29% of SVL and 1.0–1.2 times forearm length. Discs moderately expanded. Finger III conspicuously swollen along preaxial side; postaxial side rarely swollen (e.g., AMNH 98310). Preaxial side of finger II bearing distinct fringe in both sexes but not swollen. Finger III not swollen in adult females or juveniles. Fingers fringed. Metacarpal fold present, forming small tubercle proximally in some specimens (e.g., AMNH 98310). Appressed finger I longer than finger II; finger II extended to proximal edge of distal subarticular tubercle of finger III; finger IV extended to distal edge of distal subarticular tubercle of finger III. Relative finger lengths $II < IV < I < III$. Subarticular tubercles 1–1–2–2. All tubercles strongly protuberant except diffuse distal subarticular tubercle of swollen finger III in adult males; subarticular and thenar tubercles elliptical; palmar tubercle subcircular.

Shank and foot length 40–47% and 37–44% of SVL, respectively. Relative lengths of appressed toes $I < II < V < III < IV$. Toe III extended to midlevel of antepenultimate phalanx of toe IV; toe V extended to middle of penultimate subarticular tubercle. Toe webbing moderate but highly variable; in some specimens, all toes fringed but webbing absent between toes I and II and IV and V (e.g., holotype MCZ 19209); when present, webbing formula **I** 1 to 2–2 to 2½ **II** 1½–3– to 3+ **III** 2 to 2½–3 to 4 **IV** 3½ to 4+–2 to 2½ **V**. Toes weakly to strongly fringed. Discs moderately expanded. Tubercles strongly protuberant except proximal tubercle of toe IV weak and poorly defined in some specimens (e.g., AMNH 17636). Subarticular tubercles 1–1–2–3–2. Inner metatarsal tubercle elongate. Outer metatarsal tubercle subcircular, diameter roughly one-half length of inner metatarsal tubercle. Medial metatarsal tubercle present in all specimens, ranging from clearly defined, protuberant tu-

bercle to inconspicuous swelling (see Myers et al., 1991: 23–24). Outer metatarsal fold present in all specimens, not forming tubercle. Tarsal keel prominent, weakly curved, expanded proximally but not forming tuberclelike protuberance, continuous with inner metatarsal tubercle.

COLOR IN PRESERVATIVE: Dorsum brown with dark brown blotches usually concentrated medially. Pale dorsolateral stripe absent. Flank dark brown, broken only by white or cream oblique lateral stripe extending from groin midway to arm almost reaching arm insertion, broken anteriorly into elongate spots in some specimens (e.g., AMNH 124217, IAvH 3347). Ventrolateral stripe between groin and midlevel of arm insertion (i.e., not passing above arm insertion) white or cream. Entire otic region dark brown. Area below tympanum gray or pale brown, often with fine white or gray line or series of small spots extending from arm below eye and along brown or dark brown lip around tip of snout. Loreal region dark brown.

Ventral coloration sexually dimorphic (fig. 6). Adult males white or cream, immaculate or with faint brown or gray irregular stippling or mottling scattered over throat, chest, and lateral belly. Females darker than males, varying from white with brown or gray mottling or reticulation to brown with irregular white spots on throat, chest, and lateral belly. Dimorphism less marked in specimens from Cerro Azul. Juveniles immaculate white or cream.

Dorsal surface of upper arm gray or brown, with or without a dark brown transverse band just near the elbow; anterior and posterior surfaces dark brown, forming dark brown longitudinal stripes (inconspicuous in some Colombian specimens), broken ventrally by tiny white spots; ventrally white or cream. Dorsal, anterior, and posterior surfaces of forearm gray or pale brown with one to three dark brown transverse bars or blotches; concealed surface white or cream. Palmar surfaces brown; contact surfaces free of melanophores. Dorsally fingers I and II mostly white or gray with brown blotches; fingers III and IV mostly brown with small white or gray blotches.

Dorsal surface of thigh gray or brown with

two to four dark brown transverse bands that align (when limb flexed) with two or three dark brown transverse bands or blotches on gray or brown outer surfaces of shank and foot. Anterior surface of thigh gray or pale brown with well-defined dark brown longitudinal stripe; posterior surface gray or pale brown with dark brown mottling or dark brown with gray or pale brown spots; some specimens (e.g., AMNH 124216; see fig. 6) with distinct crescent-shaped pale gray or brown mark at base of thigh, extending distad along posterior surface of thigh. Ventral surface of thigh and concealed surfaces of shank and foot immaculate white or cream. Plantar surfaces brown. Toe webs and fringes with extensive scattered melanophores.

COLOR IN LIFE: Field notes made over the years by Charles W. Myers (KU and AMNH specimens) at widely scattered localities in Panama mention "golden yellow" or "gold" flash marks in the axilla, groin, and concealed surfaces of hind limbs, with these markings developing ontogenetically. For example, Myers described AMNH 98309–16 as follows: "[adult males AMNH 98309–11] with bright, golden yellow flash marks, these markings being weak or faint in other specimens," where the other specimens included two juveniles (AMNH 98315–16), two sub-adult females (AMNH 98312–13), and one very small adult male (AMNH 98314).

The ontogenetic development of flash marks was also indicated by Richard G. Zweifel, whose detailed color notes on AMNH 69845–49 and 161570–79 are summarized as follows: Dorsal ground brown, usually fairly dark and sometimes with reddish tinge; obscure darker dorsal markings present on all individuals; dark brown lateral band variably developed; lighter line separating dark brown lateral band from middorsal lighter brown [= pale dorsolateral stripe] absent; light inguinal [= oblique lateral] stripe present in all specimens, usually reaching about half way from groin to axilla, within dark lateral band (not bordering it), yellow in groin and becoming whiter anteriorly in most specimens, entirely white or yellow in some specimens; larger specimens with a few white specks along upper lip, smaller specimens with white stripe on upper lip; bright yellow flash marks conspicuously present in

larger frogs, paler in smaller ones; ground color of chin [= throat], chest, and belly grayish white in all specimens; adults with mottling of darker gray on chin and/or chest, better developed in adults than in juveniles; lower surfaces of thigh clear grayish white in all but one specimen with very light yellowish tinge; juveniles with more yellowish tinge to ventral surface thigh; bright yellow flash marks in groin and hidden surface of shank, well developed and conspicuous in adults, scarcely suggested in juveniles.

DISTRIBUTION: *Colostethus panamensis* occurs at elevations below 800 m throughout about the eastern two-thirds of Panama, including the provinces of Coclé, Colón, Darién, Herrera, Panamá, and San Blas, and in extreme northwestern Colombia in the Parque Nacional Natural Los Katios, Department of Chocó, near the Panamanian border (fig. 5).

REMARKS: Both Dunn (1933) and Savage (1968) drew attention to slight differences between specimens from eastern and western localities. Dunn (1933) separated specimens from eastern localities as *Hyloxalus* [now *Colostethus*] *fuliginosus* on the basis of their slightly more extensive toe webbing. Without comment, Breder (1946) concluded that the eastern specimens were in fact *Prostherapis* [now *Colostethus*] *inguinalis*. Savage (1968) also concluded that the eastern Panamanian specimens were not *C. fuliginosus* (which he restricted to eastern Ecuador; see also Coloma, 1995), but he listed additional differences between eastern and western samples, including distinctiveness of transverse bars on thighs, shank coloration, extent of dark mottling on throat, dorsal and flank coloration, extent of pale oblique lateral stripe, and adult SVL, as well as extent of toe webbing. Nevertheless, Savage (1968: 751–753) chose not to separate eastern and western populations as distinct species, arguing that specimens collected immediately east of the Canal Zone "are essentially intermediate between Darién and West Panamá populations and support the concept that all three samples represent the same species."

Savage (1968) did not provide collection numbers for the relevant specimens, so it is difficult to examine his conclusions. The maximum SVLs reported here are smaller

than Savage's (he reported 30 mm for males and 33 mm for females from Darién), and the available data (pooled for each sex) could not reject the hypothesis that eastern and western samples were drawn from the same population (for males $t = 1.13$, $P = 0.2650$; for females $t = 0.30$, $P = 0.7707$). The variation Savage reported in ventral coloration is likely due to sexual dimorphism, with females ventrally darker and having a more distinctive pattern than males (figs. 6–7). Distinctiveness of transverse bars on thighs, shank coloration, dorsal and flank coloration, and extent of pale oblique lateral stripe all vary among the specimens examined, but the degree of within-sample variation encompasses that reported by Savage. The degree of variation in toe webbing reported here is slightly greater than that given by Savage; however, it does not demarcate eastern and western samples and is almost fully encompassed by within-sample variation. One of the specimens with the least webbing is the holotype (MCZ 19209) from El Valle de Antón, whereas other specimens from El Valle de Antón have more extensive webbing (e.g., AMNH 124216). Also, the variation in webbing does not seem to track elevation; for example, AMNH 161579 from Cerro Azul is one of the specimens with the most extensive webbing, whereas AMNH 161576 is part of the same series and has much less extensive webbing. As such, available data do not validate the recognition of samples from eastern and western localities as distinct species.

COMMENTS ON THE IDENTITY OF *COLOSTETHUS LATINASUS*

Based on the information in the species descriptions, it is likely that the original types of *Colostethus latinasus* and *C. inguinalis* were conspecific. The holotypes were both collected along the Río Truandó by Arthur Schott on the same expedition, and Cope (1868: 137) remarked on the closeness of the two taxa. Most differences reported by Cope do not stand up to scrutiny, either because they are observably false (e.g., his claim that the tympanum of *C. inguinalis* is concealed) or are encompassed by the variation observed among specimens of *C. inguinalis*

(e.g., size⁵). The sole difference that cannot be disconfirmed is found in the generic descriptions, where Cope stated that *Colostethus* (type species: *Phyllobates latinasus*) lacks an omosternum (“manubrium”; Cope, 1866: 130), whereas in *Prostherapis* (type species: *Prostherapis inguinalis*) the omosternum consists of “a bony style, with cartilage disc” (Cope, 1868: 137). It was on this basis that Peracca (1904: 17) referred Boulenger's (1898) specimens of *C. latinasus* to *Prostherapis* [now *Colostethus*] *pulchellus*. Unfortunately, the holotype of *C. latinasus* was lost as early as 1920 (Barbour and Noble, 1920), so it is impossible to determine the veracity of Cope's report.

Regardless of the characteristics of the holotype of *Colostethus latinasus*, Savage (1968: 755) designated the adult female USNM 50198 as neotype (30.3 mm SVL; fig. 1C). Inasmuch as this specimen is not conspecific with the holotype of *C. inguinalis*, both species are valid, leaving the problem of potential generic validity to be investigated further. Minimal dissection of KU 115910 by expanding an existing slit revealed that *C. latinasus* sensu Savage possesses a fully developed omosternum (like *C. inguinalis*), but, as noted in the diagnoses above, *C. latinasus* differs from both *C. inguinalis* and *C. panamensis* in toe webbing (absent between all toes or barely detectable between toes III and IV in *C. latinasus*), ventral coloration (throat and chest brown with white spots forming mottled pattern, darker in adult males, lighter but still conspicuous in adult females; see figs. 1C and 8), and in having white (unpigmented) testes (based on adult male KU 94811). A further distinction may also be found in their ecology: *C. latinasus* is a nonriparian frog usually found on the floor of wet montane forest, including cloud forest, away from streams, whereas *C. inguinalis* and *C. panamensis* are riparian, occurring only in the immediate adjacency of streams.

It should be noted that although Savage

⁵ In his description of *Phyllobates latinasus* Cope (1863: 44) reported measurements in cm (") and mm (""), giving a length of 3 cm for the holotype. Measurements in the description of *Prostherapis inguinalis* were reported in lines, with 12 lines per inch; the length Cope (1868: 10) gave of 12.5 lines is then equal to 26.4 mm.

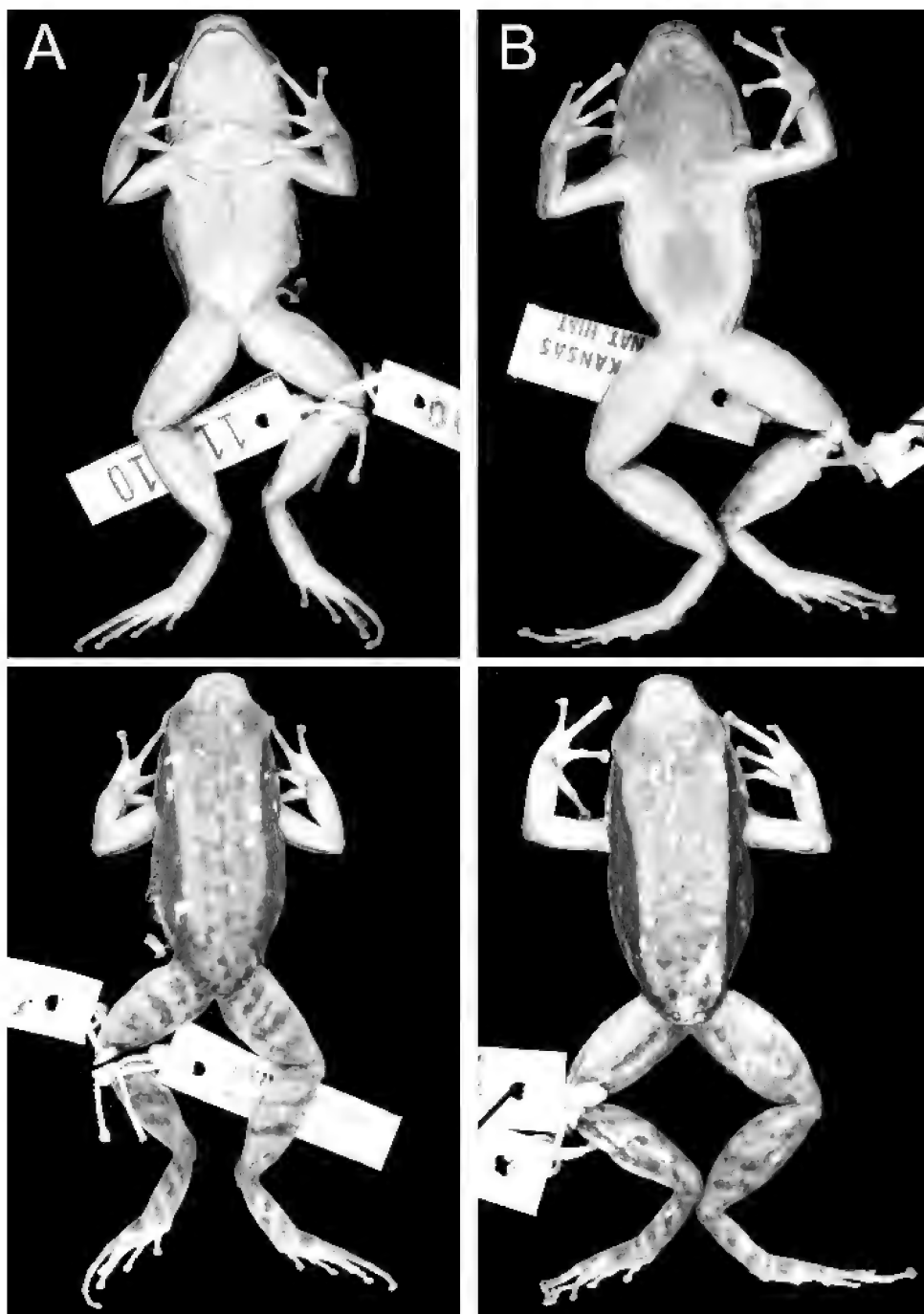


Fig. 8. Ventral and dorsal views of *Colostethus latinasus*. A: Adult female (KU 115910, 31.8 mm SVL). B: Adult male (KU 94811, 30.1 mm SVL).

(1968: 755) reported the neotype locality to be "Panamá:Provincia de Darién:Cana", these data appear to have been copied from the species index card and not the actual USNM catalog. According to Steve W. Gotte (*in litt.*, 17 October 2000),

The specimens were catalogued with Goldman's Biological Survey of Panama collection, however all four specimens (USNM 050197–050200) do not have field numbers (which the large majority of the collection has) and the collector column was clearly intentionally left blank. In the locality field "Panama" is clearly dittoed from the previous record, however "Cana" is clearly NOT dittoed from the previous record.

Consequently, for nomenclatural purposes, the locality for the neotype can only be narrowed with certainty to Panama.

Nevertheless, I examined three specimens (adult male KU 94811,⁶ 30.1 mm SVL; sub-adult female KU 115909, SVL 28.0 mm; adult female KU 115910, SVL 31.8 mm; adults shown in fig. 8) collected by C. W. Myers in 1965 and 1966 in the Serranía de Pirre between 1100 and 1440 m elevation (fig. 5; see Myers, 1969 and 1982, for locality descriptions), and these agree in all regards with the neotype (fig. 1C). Also, the fact that the neotype was cataloged in the midst of a collection made by Edward A. Goldman is at least suggestive of a general locality. Goldman's base camp was at the abandoned mines at Santa Cruz de Cana and he reached the summit of Cerro Pirre from there. Charles W. Myers (*in litt.*, 27 June 2003) doubts that *C. latinasus* occurs at Cana (at 500 m) but found it well above Cana on Cerro Pirre calling in the cloud forest above 1400 m. It appeared to be less common on the northern end of the Serranía de Pirre in the ridge-top cloud forest at 1100–1230 m. The locality of the neotype of *C. latinasus* may therefore be cited as "Panama, probably on Cerro Pirre above Santa Cruz de Cana, Darién Province".

The other specimens of *Colostethus latinasus* that Savage (1968) reported were KU 76827–76830, for which the locality is northeast of the Serranía de Pirre in the Serranía

del Darién at 1400 m on Cerro Malí (see Myers, 1969, and Myers and Lynch, 1997, for locality descriptions). I examined those specimens and AMNH 104653–104656 from the same locality, and, although they share a number of character-states (e.g., webbing absent, finger III weakly swollen, testes white, incomplete pale oblique lateral stripe present), I conclude that they are not conspecific with *C. latinasus*. The specimens from Cerro Malí are considerably smaller (four adult males are 22.9–24.6 mm SVL; four adult females are 25.5–26.4 mm SVL) and ventrally paler in both sexes than *C. latinasus*. Also, the available samples suggest that these species are isolated on separate mountain ranges. Charles W. Myers (*in litt.*, 27 June 2003) heard this species calling no lower than 1320 m on Cerro Malí. Myers also heard a few individuals calling in wet forest at 1400 m on the southwest sector of the adjacent Cerro Tacarcuna during his ascent to a camp at 1590 m. He did not see or hear this species in the forest at 1540–1660 m on Cerro Tacarcuna, nor at 1400 m during the descent 12 days later, although that expedition was made during relatively dry weather in January–February. This species will be named elsewhere.

DISCUSSION

Colostethus inguinalis is the second species of dendrobatid found in both the Chocó and Magdalena Valley regions of Colombia. The only other dendrobatid species known to occur in both areas is *Dendrobates truncatus* (Cope, 1861), although it is found predominantly in the Magdalena/Caribbean region (area B of Lynch et al., 1997) with only minor incursions into extreme northern Chocó (Silverstone, 1975). *Colostethus inguinalis* is also found in northern Chocó but extends at least as far south as about 6°45'N. Anurans generally do not lend support for the recognition of the single Chocó–Magdalena biogeographic province proposed by Hernández-Camacho et al. (1992), but sharing of species across these two regions is not entirely unexpected. Lynch and Suárez-Mayorga (2004) listed 14 typically Chocoan species that also extend into the middle Magdalena Valley, including *Bufo haematiticus* Cope,

⁶ This specimen was collected and cataloged with KU 94810, which is missing, and 94812, which was destroyed (Juán Manuel Guayasamin, *in litt.*, 13 October 2003; 3 November 2003).

1862, *Centrolene prosoblepon* (Boettger, 1892), *Eleutherodactylus gaigeae* (Dunn, 1931), and *E. raniformis* (Boulenger, 1896).

Further evidence on the systematics of dendrobatids may be found in parental care. Among the species discussed in this paper, tadpole transport has been observed in *Colostethus panamensis*, *C. flotator*, *C. nubicola*, *C. pratti*, *C. talamancae*, and the undescribed *Colostethus* sp. from Cerro Malí. Nurse frogs of *C. panamensis* (Wells, 1980b; Myers and Daly, 1983; AMNH 87293, 98317–98318, ANSP 22358) and *C. pratti* (Wells, 1981; AMNH 107170, 107172) appear to be exclusively female. Dunn (1940: 109) reported male nurse frogs for both these species (as *Hyloxalus fuliginosus* and *H. panamensis*, respectively; see Breder, 1946), but this seems to have been in error. I was unable to find the specimen of *C. panamensis* (collected by George Lee on Santa Rita Mt. in 1936, according to Dunn), but the specimen of *C. pratti* is ANSP 21800, which I determined to be a female. Both sexes have been reported to transport larvae in *C. talamancae* (Breder, 1946: 406–407, reported and figured adult male AMNH 51800 with eight tadpoles, sex confirmed by me; Silverstone, 1976: 8, reported CRE 901 [presently at LACM] as an adult female nurse frog). In *C. flotator* (Wells, 1981; Ibáñez and Smith, 1995; Savage, 2002), *C. nubicola* (Wells, 1981; Ibáñez and Smith, 1995; Savage, 2002; KU 76832, 115687), and *Colostethus* sp. from Cerro Malí (KU 76830) nurse frogs appear to be exclusively male. Insofar as all of these states have been observed throughout Dendrobatidae, their phylogenetic significance cannot yet be inferred, but they do provide additional evidence for species validity.

ACKNOWLEDGMENTS

For specimen loans and access to collections I am grateful to Ned Gilmore (ANSP), Hermano Luis A. Zamudio (CSJ), Yaneth Muñoz (IAvH), John Lynch and María Cristina Ardila (ICN), William Duellman and Linda Trueb (KU), David Kizirian (LACM), Vivian Páez (MHUA), James Hanken (MCZ), Karen Lips (SIUC), Arnold Kluge (UMMZ), Roy McDiarmid (USNM), and

Fernando Castro (UVC). Additionally, Linda Ford (AMNH), Ned Gilmore (ANSP), John Simmons and Juan Manuel Guayasamin (KU), Kent Beaman (LACM), Greg Sneider (UMMZ), and Steve Gotte and Addison Wynn (USNM) went to great lengths to provide information on the history of many specimens. Roberto Ibáñez, John Lynch, Charles Myers, Philip Silverstone-Sopkin, and Richard Zweifel shared field notes and provided access to photographs and/or unpublished data. William Duellman, Roberto Ibáñez, John Lynch, Charles Myers, and Jay Savage offered many suggestions that greatly improved the paper. I am especially grateful to Charles Myers for his thoughtful responses to my many queries. Leo Smith's expertise in digital photography and image manipulation was extremely helpful. Amanda Grant corrected the Resumen. Funding was provided by a Graduate Student Fellowship at AMNH, a CERC Faculty Fellowship at Columbia University, and NSF DEB 0309226.

REFERENCES

- Barbour, T., and G.K. Noble. 1920. Some amphibians from northwestern Perú, with a revision of the genera *Phyllobates* and *Telmato-bius*. Bulletin of the Museum of Comparative Zoology 63: 395–427.
- Boulenger, G.A. 1882. Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum. London: Taylor and Francis.
- Boulenger, G.A. 1898. An account of the reptiles and batrachians collected by Mr. W. F. H. Rosenberg in western Ecuador. Proceedings of the Zoological Society of London 1898: 107–126.
- Breder, C.M., Jr. 1946. Amphibians and reptiles of the Rio Chucunaque drainage, Darien, Panama, with notes on their life histories and habits. Bulletin of the American Museum of Natural History 86: 375–436.
- Cochran, D.M. 1961. Type specimens of reptiles and amphibians in the U. S. National Museum. Bulletin of the U. S. National Museum: i–xv, 1–289.
- Cochran, D.M. 1966. Taxonomy and distribution of arrow-poison frogs in Colombia. Memórias do Instituto Butantan 33: 61–65.
- Cochran, D.M., and C.J. Goin. 1970. Frogs of Colombia. Bulletin of the U.S. National Museum 288: 1–655.
- Coloma, L.A. 1995. Ecuadorian frogs of the genus *Colostethus* (Anura: Dendrobatidae). Uni-

- versity of Kansas Museum of Natural History Miscellaneous Publication 87: 1–72.
- Cope, E.D. 1863. On *Trachycephalus*, *Scaphiopus*, and other American Batrachia. Proceedings of the Academy of Natural Sciences of Philadelphia 15: 43–54.
- Cope, E.D. 1866. Fourth contribution to the herpetology of tropical America. Proceedings of the Academy of Natural Sciences of Philadelphia 18: 123–132.
- Cope, E.D. 1868. An examination of the Reptilia and Batrachia obtained by the Orton Expedition to Ecuador and the upper Amazon, with notes on other species. Proceedings of the Academy of Natural Sciences of Philadelphia 20: 96–140.
- Daly, J.W., F. Gusovsky, C.W. Myers, M. Yotsu-Yamashita, and T. Yasumoto. 1994. First occurrence of tetrodotoxin in a dendrobatid frog (*Colostethus inguinalis*), with further reports for the bufonid genus *Atelopus*. Toxicon 32: 279–285.
- Duellman, W.E. 1966. Aggressive behavior in dendrobatid frogs. Herpetologica 22: 217–221.
- Duellman, W.E. 1967. Additional studies of chromosomes of anuran amphibians. Systematic Zoology 16: 38–43.
- Dunn, E.R. 1931. New frogs from Panama and Costa Rica. Occasional Papers of the Boston Society of Natural History 5: 385–401.
- Dunn, E.R. 1933. Amphibians and reptiles from El Valle de Anton, Panama. Occasional Papers of the Boston Society of Natural History 8: 65–79.
- Dunn, E.R. 1940. New and noteworthy herpetological material from Panama. Proceedings of the Academy of Natural Sciences of Philadelphia 92: 105–122.
- Dunn, E.R. 1957. Neotropical frog genera: *Prostherapis* versus *Hyloxalus*, with remarks on *Phyllobates*. Copeia 1957: 77–78.
- Edwards, S.R. 1971. Taxonomic notes on South American *Colostethus* with descriptions of two new species (Amphibia, Dendrobatidae). Proceedings of the Biological Society of Washington 84: 147–162.
- Edwards, S.R. 1974. Taxonomic notes on South American dendrobatid frogs of the genus *Colostethus*. Occasional Papers of the Museum of Natural History, University of Kansas 30: 1–14.
- Evans, H.E. 1947. Notes on Panamanian reptiles and amphibians. Copeia 1947: 166–170.
- Fouquette, M.J., Jr. 1960. Notes on a collection of anurans from the Canal Zone. Herpetologica 16: 58.
- Grant, T. 1998. Una nueva especie de *Colostethus* del grupo *edwardsi* de Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 22: 423–428.
- Grant, T., and F. Castro-Herrera. 1998. The cloud forest *Colostethus* (Anura, Dendrobatidae) of a region of the Cordillera Occidental of Colombia. Journal of Herpetology 32: 378–392.
- Grant, T., D.R. Frost, R. Ibáñez D., C.W. Myers, and J.M. Savage. In press. *Hyloxalus panamensis* Dunn, 1933 (Amphibia: Anura: Dendrobatidae): proposed validation of emendment of spelling to *panamensis*. Bulletin of Zoological Nomenclature.
- Grant, T., E.C. Humphrey, and C.W. Myers. 1997. The median lingual process of frogs: a bizarre character of Old World ranoids discovered in South American dendrobatids. American Museum Novitates 3212: 1–40.
- Grant, T., and L.O. Rodríguez. 2001. Two new species of frogs of the genus *Colostethus* (Dendrobatidae) from Peru and a redescription of *C. trilineatus* (Boulenger, 1883). American Museum Novitates 3355: 1–24.
- Heatwole, H., and O.J. Sexton. 1966. Herpetofaunal comparisons between two climatic zones in Panama. The American Midland Naturalist 75: 45–60.
- Hernández-Camacho, J., Hurtado Guerra, A., Ortiz Quijano, and R., Walschburger, T. 1992. Unidades biogeográficas de Colombia. In G. Halffter (editor), La diversidad biológica de Iberoamérica I: 105–151. Xalapa, México: Acta Zoológica Mexicana.
- Ibáñez D., R., A.S. Rand, and C.A. Jaramillo. 1999. Los anfibios del Monumento Natural Barro Colorado, Parque Nacional Soberanía y áreas adyacentes / The amphibians of Barro Colorado Nature Monument, Soberanía National Park and adjacent areas. Panama: Editorial Mizrahi & Pujol.
- Ibáñez, R., and E.M. Smith. 1995. Systematic status of *Colostethus flotator* and *C. nubicola* (Anura: Dendrobatidae) in Panama. Copeia 1995: 446–456.
- ICZN. 1999. International Code of Zoological Nomenclature, Fourth Edition. London: International Trust for Zoological Nomenclature 1999.
- La Marca, E. 1994. Descripción de un nuevo género de ranas (Amphibia: Dendrobatidae) de la Cordillera de Mérida, Venezuela. Anuario de Investigación 1991: 39–41.
- Lynch, J.D. 1982. Two new species of poison-dart frogs (*Colostethus*) from Colombia. Herpetologica 38: 366–374.
- Lynch, J.D. and W.E. Duellman. 1997. Frogs of the genus *Eleutherodactylus* in western Ecuador. Special Publication of The University of Kansas Natural History Museum 23: 1–236.

- Lynch, J.D., P.M. Ruiz-Carranza and M.C. Ardila-Robayo. 1997. Biogeographic patterns of Colombian frogs and toads. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 21: 237–248.
- Lynch, J.D., and Á.M. Suárez-Mayorga. 2004. Un análisis biogeográfico de los anfibios del Chocó biogeográfico. In O. Rangel (editor), *Colombia Diversidad Biótica IV, El Chocó Biogeográfico*: 614–648. Bogotá: Instituto Ciencias Naturales, Universidad Nacional de Colombia.
- Myers, C.W. 1969. The ecological geography of cloud forest in Panama. *American Museum Novitates* 2396: 1–52.
- Myers, C.W. 1982. Blunt-headed vine snakes (*Imantodes*) in Panama, including a new species and other revisionary notes. *American Museum Novitates* 2738: 1–50.
- Myers, C.W., and J.W. Daly. 1983. Dart-poison frogs. *Scientific American* 248: 120–133.
- Myers, C.W., and W.E. Duellman. 1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. *American Museum Novitates* 2752: 1–32.
- Myers, C.W., and J.D. Lynch. 1997. *Eleutherodactylus laticarpus*, a peculiar new frog from the Cerro Tacarcuna Area, Panamanian-Colombian frontier. *American Museum Novitates* 3196: 1–12.
- Myers, C.W., A. Paolillo O., and J.W. Daly. 1991. Discovery of a defensively malodorous and nocturnal frog in the family Dendrobatidae: Phylogenetic significance of a new genus and species from the Venezuelan Andes. *American Museum Novitates* 3002: 1–33.
- Noble, G.K. 1922. The phylogeny of the Salientia I. The osteology and the thigh musculature; their bearing on classification and phylogeny. *Bulletin of the American Museum of Natural History* 46: 1–87.
- Noble, G.K. 1923. New batrachians from the Tropical Research Station, British Guiana. *Zoologica* 3: 288–299.
- Noble, G.K. 1926. The pectoral girdle of the brachycephalid frogs. *American Museum Novitates* 230: 1–14.
- Parker, H.W. 1935. The frogs, lizards, and snakes of British Guiana. *Proceedings of the Zoological Society of London* 1935: 505–530.
- Peracca, M. 1904. Rettili ed anfibi. *Bollettino dei Musei di Zoologia ed Anatomia comparata della R. Università di Torino* 19: 1–41.
- Pough, F.H., and T.L. Taigen. 1990. Metabolic correlates of the foraging and social behaviour of dart-poison frogs. *Animal Behaviour* 39: 145–155.
- Rivero, J.A., and M.A. Serna. 1989 “1988”. La identificación de los *Colostethus* (Amphibia, Dendrobatidae) de Colombia. *Caribbean Journal of Science* 24: 137–154.
- Rivero, J.A., and M.A. Serna. 2000 “1995”. Nuevos *Colostethus* (Amphibia, Dendrobatidae) del Departamento de Antioquia, Colombia, con la descripción del renacuajo de *Colostethus fraterdanieli*. *Revista de Ecología Latinoamericana* 2: 45–58.
- Savage, J.M. 1968. The dendrobatid frogs of Central America. *Copeia* 1968: 745–776.
- Savage, J.M. 2002. The amphibians and reptiles of Costa Rica: A herpetofauna between two continents, between two seas. Chicago: University of Chicago Press.
- Savage, J.M., and W.R. Heyer. 1967. Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, Central America. *Beiträge zur Neotropischen Fauna* 5: 111–131.
- Savage, J.M., and W.R. Heyer. 1997. Digital webbing formulae for anurans: a refinement. *Herpetological Review* 28: 131.
- Silverstone, P.A. 1975. A revision of the poison-arrow frogs of the genus *Dendrobates* Wagler. *Natural History Museum of Los Angeles County Science Bulletin* 21: 1–55.
- Silverstone, P.A. 1976. A revision of the poison-arrow frogs of the genus *Phyllobates* Bibron in Sagra (family Dendrobatidae). *Natural History Museum of Los Angeles County Science Bulletin* 27: 1–53.
- Simon, M.P. and C.A. Toft. 1991. Diet specialization in small vertebrates: mite-eating frogs. *Oikos* 61: 263–278.
- Toft, C.A. 1980. Seasonal variation in populations of Panamanian litter frogs and their prey: a comparison of wetter and drier sites. *Oecologia* 47: 34–38.
- Toft, C.A. 1981. Feeding ecology of Panamanian litter anurans: patterns in diet and foraging mode. *Journal of Herpetology* 15: 139–144.
- Toft, C.A. 1995. Evolution of diet specialization in poison-dart frogs (Dendrobatidae). *Herpetologica* 51: 202–216.
- Wells, K.D. 1980a. Behavioral ecology and social organization of a dendrobatid frog (*Colostethus inguinalis*). *Behavioral Ecology and Sociobiology* 6: 199–209.
- Wells, K.D. 1980b. Evidence for growth of tadpoles during parental transport in *Colostethus inguinalis*. *Journal of Herpetology* 14: 428–430.
- Wells, K.D. 1981. Parental behavior of male and female frogs. In R.D. Alexander and D.W. Tinkle (editors), *Natural selection and social behavior: recent research and new theory*: 184–197. New York: Chiron Press.

APPENDIX 1

SPECIMENS EXAMINED

The following list of specimens and localities only includes material central to the present study. Material examined for comparison is not listed.

Colostethus inguinalis ($N = 137$): COLOMBIA: **Antioquia**: Municipio Cáceres, Quebrada La Ceiba, CSJ 1844, 1846–1847, 1852, 1854, 1857–1858; Municipio Remedios, CSJ 205–207, 966–969, 1417–1420, 1692; Municipio Remedios, 400 m, UVC 7381; Puerto Berrio, MHUA 172, MHUA (PLA 26). **Boyacá**: Municipio Puerto Boyacá, Inspección de Policía Puerto Romero, Vereda La Fiebre, Quebrada la Fiebecita, ICN 47962–47968. **Chocó**: River Truandó, USNM 4349 (holotype); Upper Río Napipí, 45 min by canoe below mouth of Río Merendó (tributary of Río Napipí), ca. 60–90 m, LACM 42325–42332; trail between Río Merendó and Cerro Los Hermanos, LACM 42333; upper Río Napipí, forested hills near river on left bank, 45 min by canoe below mouth of Río Merendó, 60–200 m, LACM 42334–42340, 43955; upper Río Napipí, forested hills near river on right bank, LACM 42341–42344; upper Río Opogadó, ca. 1 hr 45 min by canoe above mouth of Río Merendó, LACM 42345–42490, 42492–42495, 42497–42521; upper Río Opogadó, between locality of 14 May 1968 [that of LACM 42345] and a point 1 hr 15 min by foot above it, LACM 42522–42526; Serranía del Baudó, Camino de Salinas, trail between Río Yupe (tributary of Río Opogadó) and Pacific coast, LACM 42528; trail between upper Río Opogadó and upper Río Napipí, LACM 42529–42530; Camino de Yupe, LACM 72003, 72009–72010. **Córdoba**: Municipio Tierralta, Alto Sinú, Quebrada El Golero, 130–180 m, ICN 39235–39236; Municipio Tierralta, Alto Sinú, quebrada sin nombre, via Cañas Finas cerca a casa de Vierney, ICN 39237–39240; Municipio Tierralta, Alto Sinú, Quebrada El Socorrer, 110–140 m, ICN 39241–39243.

Colostethus latinasus ($N = 4$): PANAMA: USNM 50198 (neotype). **Darién**: SE slope Cerro Pirre, 1440 m, KU 94811; south ridge Cerro Ci-

turo, Serranía de Pirre, 1100 m, KU 115909; north ridge Cerro Pirre, Serranía de Pirre, 1230 m, KU 115910.

Colostethus panamensis ($N = 155$): COLOMBIA: **Chocó**: Parque Nacional Natural Los Katios, IAvH [IND-AN] 3337–3370, 6206, 6208–6209. PANAMA: **Coclé**: El Valle, AMNH 69832, 69834–69835, 145344–145345, UMMZ 90655; El Valle, Río Antón, ± 650 m, 87293–87297; El Valle, Río Antón, 660 m, AMNH 124216–124217; El Valle de Antón, AMNH 50756, 59655, 59657–59659, 145344–145347, MCZ 19209 (holotype); El Valle de Antón, 2000 ft, AMNH 55518–55530, 59654; El Valle de Antón, 2000 ft, stream on N side, AMNH 55531; Middle Falls, El Valle, AMNH 52738–52739; La Mesa, El Valle, AMNH 59653; Continental Divide N El Copé, 600–800 m, $80^{\circ}36'W$, AMNH 98309–98318; 12 km N El Copé, UMMZ 147835; 6 mi NNW El Copé on Continental Divide, UMMZ 167504; 6 mi NNW El Copé on Continental Divide at sawmill, UMMZ 167505, 167511; El Copé Cloud Forest, UMMZ 148794; Parque Nacional El Copé, 700–800 m, SIUC 6928–6932. **Colón**: Río Boquerón about 2.5 km (airline) N Peluca Hydrographic Station, 150 m, AMNH 89412. **Darién**: Chalichiman's Creek, Río Sucubtí [Subcutí], above falls, AMNH 40538, 40540, 40543; Chalichiman's Creek, Río Sucubtí [Subcutí], Río Chucunaque, AMNH 40895; Chalichiman's Creek, Río Sucubtí [Subcutí], AMNH 40914, 40916. **Herrera**: Jacinto [= El Jacinto, $7^{\circ}41'N$, $80^{\circ}47'W$], 2250 ft, ANSP 22358. **Panamá**: Cerro Azul, AMNH 69845–69849, 161570–161579; near Boquerón, Candelaria and Peluca Stations, AMNH 53718; Cerro Campana, AMNH 59648–59649, 59651, 69836–69844, 161566–161569; Cerro Campana, Posado San Antonio, UMMZ 124025 (10 specimens); Cerro Campana near the top 3000 ft, UMMZ 167457. **San Blas**: Atlantic drainage, Marsh Darién Expedition, AMNH 41100.

Colostethus sp. ($N = 8$): **Darién**: Cerro Malí, 1440 m, KU 76827–76830; Cerro Malí, 1400 m, AMNH 104653–104656.